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THE PROVENTRICULAR REGION OF *MACHILIS VARIABILIS* SAY (THYSANURA : MACHILIDAE)¹

By W. W. JUDD²

Abstract

The structure of the proventricular region of the bristle-tail, *Machilis variabilis* Say, is described. Its structure is found to be intermediate in complexity between that of the simple, tubular fore-gut of the Collembola and that of the muscular proventriculus of the silver-fish, *Lepisma*.

Materials

Ten mature specimens (length of body, 1.0–1.2 cm.) of the bristle-tail, *Machilis variabilis* Say, were collected from beneath rocks in woods in the vicinity of Ottawa, Ont. on Sept. 2, 1939. They were identified with the aid of the keys and descriptions of MacGillivray (5) and Lubbock (4).

Each insect was opened carefully, with eye scissors, along the mid-dorsal line, and was then placed in Bouin's fixative for about six hours. After fixing and clearing, transverse sections (10 μ) were made of the whole insect. Sections were stained with haemotoxylin and eosin. Shrinkage of tissues was slight; the diameters of the prothorax (1.5 mm.) and mesothorax (2.0 mm.) after sectioning were the same as in untreated specimens.

The following description of the proventricular region, including the measurements of the various tissues, is based on serial sections of two specimens of the bristle-tail.

Literature

The structure of the fore-gut of various species of Thysanura and Collembola has been studied by several authors. MacNamara (6) and Lubbock (4) point out that the majority of Collembola live on decaying vegetable matter, moulds, and algae, and the latter author shows that the digestive canal is essentially a straight tube. Descriptions of the fore-gut of various species of Collembola (1, 7, 9) show that it consists of a narrow oesophagus leading into the mid-gut by a small oesophageal valve. The proventricular region shows no features to distinguish it from the rest of the fore-gut.

¹ Manuscript received May 16, 1947.

Contribution from the Department of Applied Biology, University of Western Ontario, London, Ont. Part of a thesis submitted for the degree of Master of Arts of the University of Western Ontario.

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Newcomer (8) studied the digestive system of the silver-fish, *Lepisma*, and speaks of it as "including a remarkable muscular crop, the posterior end of which protrudes into the mid-intestine". Gray (2) describes this crop as "a spherical gizzard provided with six teeth". Lubbock (4) also points out that the "crop" has six horny teeth. It is thus evident that the gizzard (proventriculus) is a well developed structure in *Lepisma*.

Description

In *Machilis variabilis* Say the oesophagus occupies the prothorax and mesothorax (Fig. 1 - Oes.). It is surrounded by four lobes projecting forward from the mid-gut (L). These lobes are similar in size and position to the four gastric coeca in the alimentary canal of *Petrobius* described by Imms (3). In the prothorax the oesophagus is about 130μ in diameter and is surrounded by a single sheath of circular muscle $3-4\mu$ thick (Fig. 2 - CM). The epidermal layer is composed of a single layer of cells roughly cuboidal in shape and $5-10\mu$ thick (EP). The sclerotized intima (I) is composed of two layers, an outer one ranging from 1 to 10μ in thickness, and an inner one of a constant thickness of 1μ . It is thrown up into longitudinal ridges of irregular shape. In the posterior part of the prothorax the diameter of the oesophagus is about 140μ and the sheath of circular muscle surrounding it is about 1μ thick (Fig. 3 - CM). The ridges of the intima in the lateral walls of the oesophagus are flattened, while dorsally and ventrally the intima projects into the lumen, forming dorsal and ventral ridges (Fig. 3 - DR, VR), which almost fill the lumen.

In the fore part of the mesothorax the posterior end of the oesophagus forms the oesophageal valve (Fig. 4 - Oes. V.). It is surrounded by two lobes of the mid-gut (L). The vertical diameter of the valve is about 180μ and the transverse diameter about 90μ . In this region the dorsal and ventral ridges of the oesophageal valve touch one another and are broadened laterally to touch the lateral walls. Consequently the lumen is almost obliterated (Fig. 5). A transverse section of the oesophageal valve (Fig. 5) shows, on the outside, the irregular layer of intima (Iii). Inside this layer are two layers of epidermis (EP) separated by narrow bands of circular muscle (CM). The outer layer is continuous with the much larger cells of the mid-gut (MG). The inner layer supports the inner sclerotized intima of the valve (Ii).

FIG. 1. Transverse section of the prothorax.

FIG. 2. Transverse section of the oesophagus in the prothorax.

FIG. 3. Transverse section of the oesophagus in the posterior part of the prothorax.

FIG. 4. Transverse section of the mesothorax.

FIG. 5. Transverse section of the oesophageal valve.

CM—Circular muscle; DR—Dorsal ridge of oesophagus; EP—Epidermis; I—Intima of oesophagus; Ii—External intima of oesophageal valve; Iii—Internal intima of oesophageal valve; L—Lobe of mid-gut; MG—Cells of mid-gut; Oes.—Oesophagus; Oes. V.—Oesophageal valve; VR—Ventral ridge of oesophagus.

Fig.1

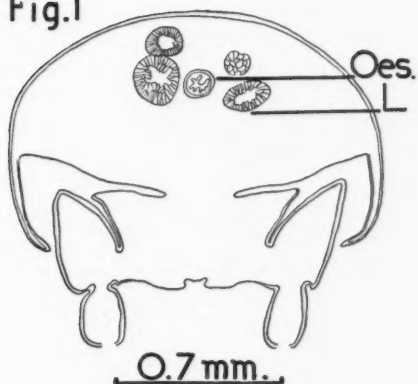


Fig.2



Fig.3

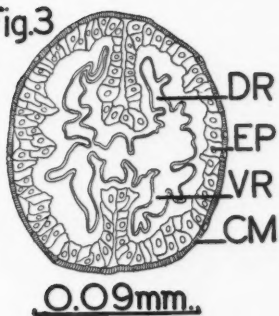


Fig.5

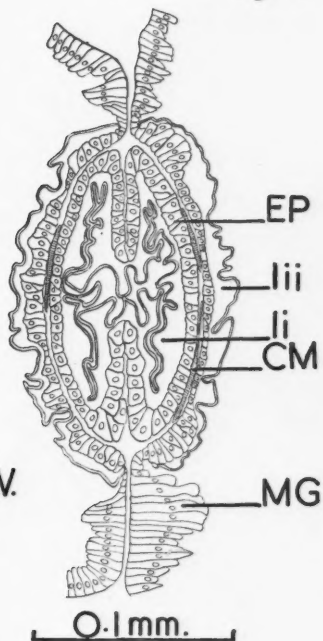
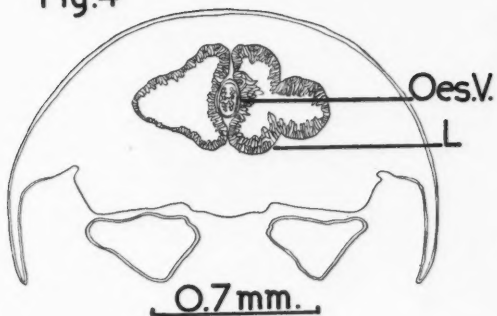


Fig.4



The foregoing description indicates that the proventricular region of *Machilis variabilis* Say is intermediate in complexity of structure between that of the Collembola and that of *Lepisma*. In the former the proventricular region is not to be distinguished from the tubular oesophagus. In the latter the proventriculus is a well defined structure bearing six horny teeth. In *M. variabilis* the proventricular region shows no abrupt separation from the rest of the fore-gut, but bears internally strong dorsal and ventral ridges that almost completely obliterate the lumen.

Acknowledgment

The writer wishes to express his gratitude to Prof. J. D. Detwiler for his guidance in this work.

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THE TIMBER WOLF IN THE ROCKY MOUNTAIN NATIONAL PARKS OF CANADA¹

BY IAN McTAGGART COWAN²

Abstract

The wolf (*Canis lupus occidentalis*) population of the Rocky Mountain National Parks of Canada, an area of 7000 square miles of mountainous terrain, was studied from 1943 to 1946. During that time it approximated a density of one wolf to between 87 and 111 square miles of potential range, which was reduced to about 10 square miles per wolf during late winter by contraction of available range. The range is heavily populated with the wild ungulates, *Ovis canadensis*, *Oreamnos americanus*, *Alces americana*, *Rangifer arcticus*, and *Odocoileus hemionus*. Many of the winter ranges are grossly overstocked. The annual diet of wolves in the area has consisted of 80% big game, with elk alone contributing 47%. Mule deer contribute another 15%. Although bighorn sheep are in abundance and available they are little hunted by wolves. Eighteen per cent of the annual diet consists of rodents, of which snowshoe hare and beaver are the two most important. Wolves are unevenly distributed and many game herds have been living without wolf pressure. Comparison of the vital statistics of game herds living with and without wolf predation reveals no discernible difference in the survival of young or in the sex ratios within the two groups. It is concluded that under existing circumstances the wolves are not detrimental to the park game herds, that their influence is definitely secondary, in the survival of game, to the welfare factors, of which the absence of sufficient suitable winter forage is the most important.

In the spring of 1943, when I began a series of wildlife studies in the Rocky Mountain National Parks of Alberta and British Columbia, I was given to understand that the apparent increase in the numbers of predatory mammals in these parks was arousing concern among certain groups interested in the ungulate mammal populations of the parks.

Hand in hand then with the gathering of data upon the ungulate mammals of the parks went the painstaking and often tantalizing task of gathering data relative to carnivores. The information upon wolves and their activities in the parks accumulated during the studies is presented herewith.

The study of wolves in the heavily timbered mountainous terrain that makes up so large a part of the area of the Rocky Mountain Parks of Canada presents many difficulties. One seldom sees the animal that is the main subject of his inquiries and must perforce be content with data gleaned from sources other than direct observation of the principals. Tracks there are aplenty, kills can be found and scats collected, and it is upon these and similar sources of data that one must depend in the main.

The investigation of wolves therefore fell into several different phases.

1. To determine what the wolves were eating, scats were collected and analysed.

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Contribution from The Department of Zoology, University of British Columbia, Vancouver, B.C., and National Parks Bureau, Department of Mines and Resources, Ottawa, Canada.

² Professor of Zoology, University of British Columbia.

2. In an attempt to qualify the information obtainable from scat analysis special effort was made to determine the circumstances surrounding the killing of certain species and individuals among the ungulate and rodent populations of the park. Kills were examined wherever possible and data secured on the age class and probable physical condition of the victim.

3. Tracks were followed and the behaviour of the wolves studied as it was betrayed by their footprints.

4. In an attempt to arrive at a reasonably accurate estimate of the year by year population of wolves in the parks and their seasonal movements the good offices of the various park wardens were sought. Many of these men went out of their way to obtain counts of individuals in different parks and to chart the movements of these groups in their respective districts.

5. Certain of the wardens either by reason of peculiar local conditions or more than ordinary personal enthusiasm were able to make first hand observations that contributed importantly to our information on the wolf and its ways. I have drawn extensively upon the factual information gleaned from these men and have acknowledged all such material wherever it is used.

These have been the sources of the direct information on wolf populations and behaviour, subjects vital to the proper understanding of the position of the wolf in the biological society of which it is probably the most important influent. Equally important, in the present instance, is the appraisal of the over-all influences of wolves upon the prey species. The local circumstances in the Rocky Mountain parks offered one useful possibility of examining this latter circumstance. Coyotes, mountain lions, and grizzly bears were found to be fairly evenly distributed over most of the areas under study. The larger ungulates were with few exceptions widely distributed. Wolves on the other hand are absent from some large areas—abundant in others. It was possible then to study populations of many of the ungulates living under approximately equivalent circumstances except for the presence or absence of wolves. Selected areas presenting these contrasting circumstances were given special study and the vital statistics of game herds living with and without wolf pressure assembled for comparison and study.

The Study Area

The Rocky Mountain Parks of British Columbia and Alberta consist of Jasper Park, with an area of 4200 sq. miles; Banff Park, 2400 sq. miles; Kootenay Park, 527 sq. miles; Yoho Park, 507 sq. miles; and Waterton Lakes Park with an area of 286 sq. miles. The first four of these occupy contiguous territory, the two first on the Alberta side and the two latter on the British Columbia side of the interprovincial boundary. Together they constitute the largest single reserved area on the North American continent. They extend the full width of the main range of the Rocky Mountains from the region of the 51st parallel to 53° 30' north latitude. Waterton Lakes Park, the smallest of the five, is situated in the southwesternmost corner of Alberta, with its southern boundary on the 49th parallel of latitude.

The wolf population of Waterton Lakes Park is so small that it is unimportant in the present study.

The entire study area lies in the floral association leading to a spruce forest climax through various seral types, which, as forests, begin as jack pine or aspen stands at lower elevations, balsam forests at and near timber line. Elevations above 7000 ft. are for the most part above tree line. Here the spruce and balsam forests give way abruptly to extensive alplands upon which the lower areas support a heavy growth of a half a dozen or more species of willows (*Salix*). These become progressively shorter in stature with altitude and give way to the heaths (*Phyllodoce* and *Cassiope*), the crowberry (*Empetrum nigrum*), and many flowering plants, short grasses, and sedges at still higher levels.

Along certain of the lower valleys, such as the Athabaska and Brazeau in Jasper, the Red Deer, Panther, and Bow in Banff, there are patches of grassland usually with greatly varied relief. Open, flat land is virtually nonexistent. Rockslides and lakes are abundant at all elevations.

The lowest elevations in Jasper Park are about 3300 ft., those in Banff almost 1000 ft. higher. The snow lies late in the spring and for this reason, wolf denning takes place in the timbered areas of the park and by far the largest part of the wolf's life is spent in country in which long range visibility is impossible.

Two races of wolves contributed to the population of the area under study during the early period of its invasion by white men. The areas now included in Jasper Park probably supported a population of the Mackenzie Valley wolf (*Canis lupus occidentalis* Richardson), while the Waterton Lakes area was inhabited by the Northern Rocky Mountain wolf (*Canis lupus irremotus* Goldman).

Specimens of *occidentalis* are listed by Young and Goldman (12) from Edmonton, and from 50 miles SW. of Smith Landing, Alta., and it is probable that the contiguous Rocky Mountain region was inhabited by the same race.

Southern Alberta, north to Calgary, was within the range of *irremotus* and Young and Goldman (12, p. 448) list specimens from Calgary, Gleichen, Lethbridge, and 25 miles southeast of Lethbridge. It can safely be assumed that this was the race entering the Waterton Lakes area.

As will be detailed later, wolves were exterminated in the latter region about 1922 and are but now reappearing. The Northern Rocky Mountain wolf (*irremotus*), as compared with the Mackenzie wolf (*occidentalis*), was a smaller animal, with significantly smaller skull and lighter teeth. It was also a 'grey' wolf, and gave rise to very few black individuals.

Occidentalis, on the other hand, is a larger wolf producing many blackish or black individuals.

In the winter of 1943-44 one black wolf and in 1944-45 two wolves were known to be ranging in the area adjacent to and within the eastern edge of Waterton Lakes Park. One of these, a black male, was shot. The skull of

this specimen has been available for study and proves to be just within the size range of *irremotus* in all but 2 of 15 measured features but in the sum of all characters to be referable to the race *occidentalis*. It would seem then, that the northern race has invaded the territory previously occupied by *irremotus* and that the current recrudescence in the wolf population of the Rocky Mountains does not reflect a reappearance of the latter race. It is unlikely that the race was completely extirpated, but it may well have been so reduced in numbers in the foothills and mountains of southwestern Alberta through persistent hunting that *occidentalis*, developing an augmented population pressure in this or the last cyclic peak, has inundated the remaining population of *irremotus* and thus extirpated the race.

Corroborative evidence of this is indicated by the characteristics of the only specimen taken in recent years in that part of the former range of *irremotus* south of the 49th parallel. This animal, taken in Gallatin County, Montana, in 1941, is noted by Young and Goldman to be as large as individuals of *occidentalis* except for lighter dentition. The published measurements of the skull of this specimen reveal that even the dentition comes within the normal range of variation in *occidentalis*. There are therefore no grounds for referring this specimen to any other race. It is suggested therefore that this individual was merely the southernmost wanderer from the current invasion from the north and was indeed a specimen belonging to the race *occidentalis*.

Five specimens from the Yellowhead Pass area of British Columbia and Alberta in the Museum of Zoology, University of British Columbia, are *occidentalis*.

Physical Characteristics

The general form of the wolf is too well known to require description here; however, size data and information concerning colour and the proportions of various colour phases in the general population are scarce in the literature.

Several wolves were destroyed in Jasper Park during the years between 1942 and 1945 but for the most part these were disposed of before I was able to make any examinations.

Two young adult males taken at Decoigne, Alta., in 1944 were measured and weighed. External measurements of these were total length: 1880 mm., 1885 mm.; tail: 470 mm., 460 mm.; hind foot: 290 mm., and 280 mm. The larger of the two weighed 120 lb., the smaller 110 lb. A female shot in the same area on Apr. 13, 1944, was estimated to weigh approximately 80 lb.

A two year old female shot at Miette in November 1945 measured total length, 63 in.; tail, $18\frac{1}{4}$ in.; hind foot, $10\frac{3}{4}$ in.; ear, $4\frac{3}{4}$ in. An adult female shot at Decoigne on June 12, 1946, measured total length, 63 in.; tail, 17 in.; hind foot, 11 in.; ear, $4\frac{1}{2}$ in.; weight, 83 lb.; another adult female taken at Devona in December 1945 measured total length, 63 in.; tail, $18\frac{1}{2}$ in.; hind foot, $10\frac{3}{4}$ in.; ear, $4\frac{3}{4}$ in.

An adult male wolf shot in the same place on May 10, 1944, measured total length, 1825 mm.; tail, 475 mm.; hind foot, 275 mm.; and weight, 140 lb. with its paunch full.

A large wolf killed by Warden Frank Wells on Buffalo Prairie and weighed by him in the presence of several witnesses scaled 172 lb. This animal was distended with the load of elk meat in its stomach.

In September 1944 Warden White of Decoigne took a male pup weighing 70 lb., including a full stomach of elk meat. A female pup dug out of its den by Warden Chas. Page and examined by me on July 10, 1946, weighed 19 lb.

Colour

The colour of the wolves of the Rocky Mountain Parks is most variable, palest animals are almost white, darkest animals are almost black. The largest colour group is dark grey, the occasional individual quite brownish.

The grey and black colour phases do not seem to be mutually exclusive colours inherited en bloc. Some individuals are almost exactly intermediate between the two extremes.

A tabulation of the colours—either as grey or as black—of all wolves reported to me during the years 1944-46 reveals that, of 80 wolves seen by the various wardens of Jasper and Banff and by members of my party during this period, 44 or 55% were black and 36 or 45% grey.

This appears to be a higher proportion of blacks than hitherto reported in any North American subspecies of *Canis lupus* with the possible exception of *C. l. ligoni* from the islands of southeastern Alaska. It approximates the condition reported by Murie (9) in Mount McKinley Park, Alaska.

History

It is probable that wolves have always been present, in recent time at least, in small numbers, in certain parts of the study area. The earliest wolf record for the region concerns the great dire-wolf of Pleistocene time. In July, 1945, I picked up a fossilized tooth of this wolf among some gravel weathered from the higher peaks and lying near the middle of the Castleguard Icefield.

In more recent time the earliest explorers make casual mention of the presence of wolves in the Athabaska Valley northeast of Jasper.

At the time that serious biological studies in and adjacent to Jasper Park were begun, wolves were scarce. For example Loring, in the early autumn of 1896, reported (10) that he occasionally saw tracks of timber wolves in the country between Jasper House and the Smoky River. He heard one at Grand Cache River on Sept. 5.

Hollister (6) states that at the time of his visit to the Jasper region wolves were very scarce and reports Lewis Swift, long a resident at Henry House, as having killed but two in 19 years.

It is pertinent to note that the period in question was also one of great game scarcity. Elk were gone from the entire area now occupied by

the Rocky Mountain Parks; moose, sheep, and deer were scarce; and only caribou and goat were present in fair numbers. These species usually winter at too great an altitude in this region to provide suitable winter food for wolves.

Authentic information on the changing status of wolves in this region in the period between 1912 and the present is difficult to obtain. Jack Hargreaves has supplied me with some figures obtained by himself and his brothers during many years in the Rocky Mountains adjacent to Jasper. He states that in 1914 two wolves appeared on the upper reaches of the Whirlpool River and ranged over the summit into the Fortress Lake area. In two years' time this band had become seven or eight individuals. They were subsequently poisoned.

In 1917 many wolves appeared along the Moose River and in this and the next year or two the population seemed to be near a peak. In 1918 Roy Hargreaves and a companion saw upwards of 40 wolves, most of them at one time, along the Wapiti River, a tributary of the Peace River, 150 miles or so map distance north of Jasper.

There is a gap in our data from 1918 to 1940. During this period, apparently no records were kept of wolf numbers or distribution in Jasper Park. Wolves were absent from Kootenay and Yoho Parks except for occasional travelling individuals. Evidence discovered in 1946 reveals that a pair of wolves had denned for at least eight years in the Panther River valley about six miles below the warden cabin.

In Jasper Park, at the present time, wolves are present during all seasons of the year along the Miette River from Yellowhead Pass eastward along the Athabaska from the junction of the Sunwapta to the confluence of the Moosehorn and Athabaska near the northern edge of the eastern boundary. From Honeymoon Lake to Snaring the wolves range on both sides of the river but below Snaring they are almost confined to the country west and north of the Athabaska. Just one wolf has been seen from time to time on the south side of this river on the area adjacent to its confluence with Rocky River.

Wolves occur up Whirlpool River during all seasons as they do also along the Brazeau and the lower reaches of the Snaring River and the Snake Indian River below Willow Creek.

Summer range, from which the wolves migrate during periods of deep loose snow in the winter months, includes the upper Snake Indian, Topaz Creek, Moose River, and the valley of the Smoky River.

There are extensive areas yet without a wolf population. For example there are no wolves along the valley of Rocky River, along the Maligne Valley above the canyon, along the Cairn or upper Southesk Rivers, in the Tonquin Valley, and at the head of the Athabaska above the Sunwapta.

Game is plentiful in several of these areas and it is difficult to explain the peculiarity of wolf distribution in these parts.

In Banff Park there is a small resident population along the Saskatchewan River and along the lower parts of the Howse and Mistaya Rivers. The first wolves to enter this region, two in number, did so in the winter of 1942-43.

In 1943 there was a small resident population in the vicinity of Ya Ha Tinda Ranch and along the Red Deer River from the ranch to Scotch Camp opposite the mouth of Divide Creek. Wolves made periodic incursions into other parts of the eastern edge of the park. In 1943 they ranged up the Panther as far as Windy Cabin at the mouth of Whigmore Creek but no sign of their presence on the Panther was noted in 1945. As already stated, in July, 1946, while investigating a wolf den near the Sulphur Springs in the Panther River Valley, we found other old and new dens from which it was obvious that there has been a pair of wolves denning in this valley for at least eight years, possibly much longer. In the winter of 1944-45 three individuals came up the Ghost River to Minnewanka Lake but returned without making a kill. In 1943, 1944, and 1945 single animals were seen at Bow Summit, Goat Creek, and in the Bow Valley 18 miles west of Banff. During the winter of 1945-46 a group of five or six wolves hunted the Clearwater Valley; in the spring they denned five miles below the Park boundary.

Wolves have apparently been rare on the western slope of the Rockies at least through the period for which there is any record available. As outlined by Munro and Cowan (7), there are but two records of the presence of wolves in Kootenay Park. In 1906 two wolves came up river from near Canal Flats and crossed through the park. Again, in 1936 or thereabouts, Mr. V. H. Lord heard wolves howling and saw one of them near Vermilion Crossing.

The only recent record for Yoho Park is that of a single individual reported to me by Park Warden Nicholson. This animal came up Beaverfoot River in the winter of 1942-43 and it—or another—was killed two or three days later farther down the Kicking Horse Valley, just outside the Park.

Information on the Waterton Lake area was obtained from F. H. Rigall of Twin Butte, Alta. Grey wolves used to be fairly common in the region. In 1921 increasing depredations upon domestic livestock led the stockmen to employ a noted wolfer, H. Rivière. As a result of this man's activities wolves were locally extirpated and did not reappear until 1943, when one black individual entered the area. In 1944 two black wolves were present but the male was shot at a beef carcass killed by grizzly bear within Waterton Lake Park.

Populations and Seasonal Movements

Inasmuch as the writer was able to undertake only brief periods of winter work in the parks, when snow conditions made it possible to determine most easily local populations and movements, a large part of the data gathered relative to this subject comes from the Park wardens of Jasper and Banff National Parks.

There have been changes in the local distribution of wolves from one year to the next and as these throw some light upon the factors influencing movements the local situations will be given in detail.



FIG. 1. Jasper Park, Alta.

In the valley of the Smoky River, Warden F. J. McGuire reported in 1943 that during the previous two winters, after the snow became crusted, there were three groups of wolves working the valley periodically. One consisted of seven animals, one of two, and one was a single individual. These wolves each came down the valley approximately once a month. The last wolf tracks seen in the Smoky Valley in 1943 were those of a pack of 13 or 14 that came up the Smoky and over on to the Moose River on Dec. 15. There were no wolves present during the late winter and spring. In the winter of 1944-45 the snow lay deep and soft over the entire valley until late March and the wolves remained outside the park until the month of April when a few entered, coming up river. In the winter of 1945-46 a band of five or six wolves came up the Smoky from outside the park in December. The only other wolves seen in that warden district during the winter were three in January 1946. After several unsuccessful attempts to kill moose they returned down river and left the park.

There is a small summer population of wolves in the Smoky Valley and its subsidiary stream valleys. In August, 1943, there were tracks of at least

three different individuals on Byng Pass between the head of Twintree Creek and the head of the Snake Indian River. Two wolves worked the Byng Pass country (Fig. 4) during the summer of 1944 but produced no pups.

There is no information available on the region west of the Smoky Valley to the interprovincial boundary.

Wolves summer in the upper part of the Snake Indian Valley, including Blue Creek Valley, and stay in the autumn until snow conditions render travelling difficult. In 1942 they stayed until mid November and then withdrew down the valley. In 1943 Warden R. Jones found wolves working the upper Snake Indian and Blue Creek Valleys until almost Christmas time, when they moved down river; they did not return until early May. The largest band noted in the valley in the winter of 1942-43 consisted of 11 wolves. At different times during the early winter tracks of three were seen at Hoodoo Creek and again at Willow Creek. In this spring movement six wolves passed up the Snake Indian River to an undetermined destination beyond Hoodoo Cabin and were not seen again. There were no signs of recent wolf activity in the vicinity of Blue Creek in late May, 1944.

In August, 1943, wolves were heard howling near Blue Creek cabin and tracks of three individuals were seen along the trail to Topaz Lake. There were also tracks of three on Byng Pass, but whether these two occurrences represent the same individuals is not known. They are less than 15 miles apart. In October, 1943, Warden R. Jones saw a large pup wolf at Blue Lake at the head of Blue Creek.

At Willow Creek, in the Snake Indian Valley, there is a resident group of wolves that has numbered four or at the most five individuals constantly during the past three years. Apparently no pups have been produced by this group during this time. They apparently range a fairly small area from Rock Lake up Rock Creek to Mowitch Creek and along the flats bordering the Snake Indian, perhaps two or three miles beyond the confluence of Deer Creek with the River. The total area of their normal year round range apparently does not exceed 50 square miles.

The population of wolves wintering along the Athabaska Valley from Buffalo Prairie to Miette cabin has increased during the three years of this study. In the winter of 1942-43 nine wolves wintered on the benches adjacent to Devona (Fig. 6) and the mouth of the Snaring. These consisted of a group of four and a single animal and apparently two pairs though one of the pairs periodically joined the group of four.

A group of six seen on Pyramid Lake in the early spring was almost certainly the same group reported by Warden Bert White of Decoigne as moving down the Miette past his warden station at approximately monthly intervals. There was apparently another small pack concentrating its activities on Buffalo Prairie. In 1943, then, there were possibly 21 wolves wintering in or periodically entering the Athabaska Valley below Athabaska Falls, and these, with four at Willow Creek, four or five on the Brazeau, six or seven on the

Upper Athabaska and Whirlpool, and the 10 to 13 that moved up the Smoky in December, make up the probable total population of Jasper Park in the winter of 1942-43, a population of from 45 to 50 individuals.

During the summer of 1943 wolves apparently denned in the vicinity of Yellowhead Pass or Decoigne. During the last week in August four wolves were seen in close pursuit of a cow moose in this area; tracks were noted from time to time. Warden White of the Decoigne area during 1944 shot or snared nine wolves at Decoigne, including two pups taken in September of that year. None was resident there in the summers of 1944 and 1945 and the travelling band in the winter of 1944-45 was down to four individuals. Disease, as will be mentioned later, probably had some part in this reduction. In the summer of 1946 wolves were present at Decoigne and an adult female was shot.

In the winter of 1943-44 a band of four wolves worked the benches adjacent to Devona, two more ranged from Devona to Miette, and a single animal roamed the area generally. Six wolves left the valley in early May and moved, almost without pause, the 56 miles from Devona to Hoodoo Cabin and passed on up toward Byng Pass. The summer of 1946 first saw an established population remaining on the Athabaska Valley winter ranges. In May and June fresh wolf tracks were continually present on the Maligne horse range and in the valley of Vine Creek.

Warden Frank Wells in January saw tracks of two small packs, one of five and one of seven, on the Buffalo Prairie area (Fig. 5) under circumstances that led him to believe they were different bands. He also believed that the dozen or so wolves that ranged the upper Athabaska and Whirlpool areas that winter did not include the Buffalo Prairie packs. In January, four wolves came down Poboktan Creek and down the Banff-Jasper Highway as far as the Athabaska Falls cabin. At Decoigne wolves were active in October but they left during the latter part of the month and did not return until about Christmas time. About ten came through then but moved on and wolves were not again seen until Mar. 31 when from seven to nine entered the area. The pack split up and apparently settled in for the summer. It was at this time and during the succeeding eight months that the nine wolves were taken by Warden White. These Decoigne wolves are almost certainly part of the groups recorded as wintering on the Athabaska Valley.

The summarized count of wolves in Jasper Park in the winter of 1943-44 then would be: along the entire Athabaska Valley, approximately 30; Brazeau Valley, 4 or 5; Willow Creek, 4; or a minimum of 38. If we consider the 13 that came up the Smoky on Dec. 15 as the same as the group (estimated at about 10 animals) that came down the Miette a few days later—and there is good reason to take this view, as when last seen on the Smoky the pack was heading for Moose River, which in turn would take the pack down to Yellowhead Pass and on to the main wolf run through Decoigne—and if we regard this band as made up of animals not already tallied we can add

this number, and also the four that came down Poboktan Creek in January and arrive at a maximum population figure of 55.

The winter of 1944-45 found the wolf population slightly smaller. As already mentioned, snow conditions in the Smoky Valley kept the wolves at lower elevations and outside the park. F. A. McGuire reported that a pack of six or seven was working the winter ranges just below the park boundary most of the winter.

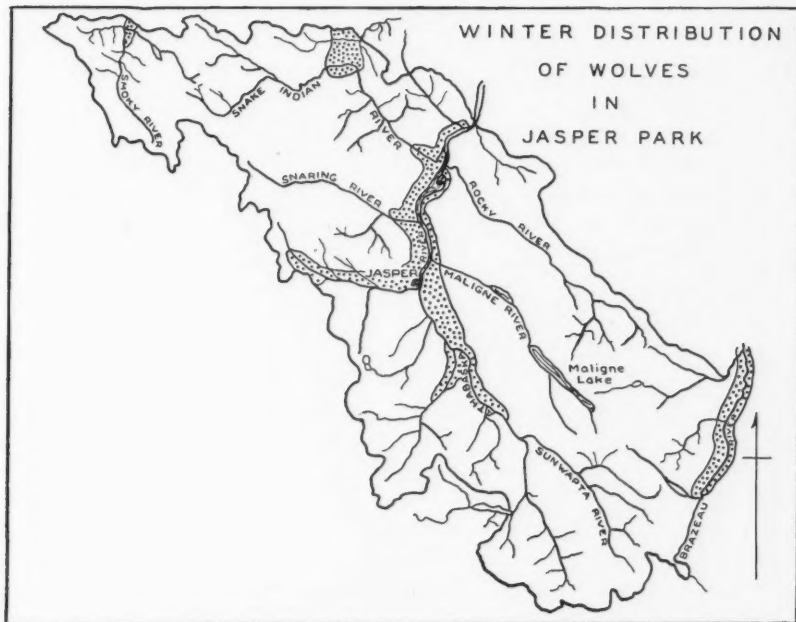


FIG. 2. Winter distribution of wolves in Jasper National Park.

Frank Wells found that a group of about seven ranged from Athabaska Falls to the Whirlpool River. This is doubtless the same pack that Warden George Camp reported as traversing the Whirlpool district at fairly regular intervals during the winter. Camp was sure of but five animals in the group. On each occasion that these wolves entered his area they came from the west and moved down the river as far as Moab and Otter Creeks, where they crossed over toward Geraldine Lakes and the Athabaska River above the falls.

On one or two occasions another pack of five or six came up the Athabaska from Buffalo Prairie, following the route of the highway to the falls area.

The presence of this group of five on Buffalo Prairie is confirmed by Frank Wells, who also suspected the presence of a pair running separately from the other five. There was another group of two or three in the Honeymoon Lake area.

The Decoigne area was visited periodically by four wolves; five ranged the Devona flats and benches, two lived in the Miette region, the same lone wolf present during the three previous years was still in the Devona-Miette area and it was probably this individual that was seen by Warden Brasnett and some others near Talbot Lake and the mouth of Rocky River. The Willow Creek band this winter numbered five and Warden J. St. Marie was able to confirm my previous estimates of the wolf population of the Brazeau River as five animals. It thus appears that the winter population in the Athabaska Valley in 1944-45 was about 23 wolves while the approximate population of Jasper Park was between 33 and 39 animals.

All these estimates are based upon the assumption that there are no wolves living through the winter in the area drained by the Snaring River. Nothing is known of the wildlife conditions of this region, but what has been reported of the terrain and its winter conditions leads to the assumption that wolves would probably be unable to winter in it.

Minimum and maximum population estimates for Jasper Park between 1942 and 1946 were:

1942-43	Minimum	45	Maximum	50
1943-44	"	38	"	55
1944-45	"	33	"	39
1945-46	"	38	"	48

If we assume that the maximum figures represent the true conditions, the density figure for Jasper National Park has been approximately one wolf for every 87 sq. miles. If the minimum figures are closer to actuality the density, based upon the area of summer range, was 111 sq. miles per wolf. At the time of maximum winter compression, however, this population is present on an area that averages approximately 10 sq. miles per wolf.

It is more difficult to estimate the population of wolves that from time to time enters the boundaries of Banff Park. Much of the park has been virtually without winter patrols and as a result there is less known of winter wildlife conditions in it than in any of the other Rocky Mountain Parks.

Only on the Saskatchewan and Panther Rivers was there evidence of a resident wolf population in 1943 (Fig. 3). In that year, also, wolves were present in summer on the Ranch and adjacent areas as well as on Snow Creek. The total of wolves periodically entering Banff Park that winter did not exceed 12 or 13 individuals. In 1944-45 evidence indicated that perhaps four wolves had been working in and out of the Park along the Red Deer and Panther Rivers. Five were seen at one time near Saskatchewan Crossing. To reach a total figure we should perhaps add the lone wolf reported to be in the Bow Valley and the three that spent a few hours in the Park on the eastern end of Lake Minnewanka. This would give a total of 13 again for the 1944-45 winter, or 10, neglecting the last trio. There may have been a slight increase in 1945 as the best available figures for the wolves entering Banff Park during the winter of 1945-46 indicate a minimum population of 12, a maximum

possible of 18. This year saw wolves become established in the Clearwater Valley where they ranged into the Park throughout the year.

The early winter of 1946-47 saw the establishment of a pack of seven to nine wolves in the Bow Valley 12 miles west of Banff marking a new extension of range southward in this Park.

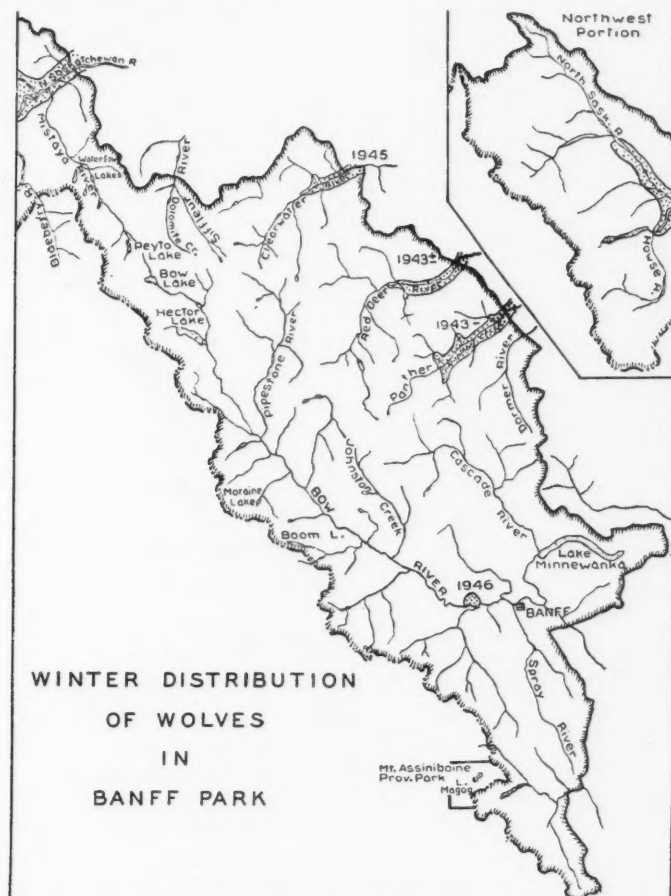


FIG. 3. Winter distribution of wolves in Banff National Park. Dates indicate years in which resident populations became established.

Movements

As has been indicated above, there is considerable variation in the amount of seasonal movement undertaken by various groups of wolves. During the summer months, when winter hunting packs are broken up and the animals hunt in ones and twos, there is evidence that certain wolves still live a roving

existence. For instance in the Brazeau Valley in 1944 two wolves had preceded us all the way down the trail from Brazeau Lake Cabin to six miles or so below Isaac Creek, a total distance of some 22 miles. Sign along this trail, both then and in 1943, showed this to be a regular travel route.

Other groups of wolves are fairly sedentary during the summer. For instance in 1943 and again in 1944 there were two or three wolves almost constantly present on Byng Pass and up Blue Creek. The summer of 1944 saw a relatively sedentary group working about 10 miles of the upper Miette Valley adjacent to Decoigne. There are always wolves on Buffalo Prairie—in 1945 these consisted of at least three adults and the pups of one pair.

Certain of the wolf groups remain relatively sedentary even during the winter months. For example the Willow Creek group of four individuals in 1943 and 1944, five in 1945 is apparently constantly on an area of some 72 sq. miles.

As mentioned above, there are wolves present on Buffalo Prairie throughout the year, and, inasmuch as the area is hemmed in by roads on the north, west, and south and backed against the mountain on the east, it is possible to keep fairly close watch on the movement of wolves into and out of the area. There are transient bands there from time to time but the resident animals roam an area of approximately 55 sq. miles.

Other groups become transient during the winter. Possibly they are wolves that summered at altitudes unsuited for winter range, either because of snow depth or because of efflux of game. These groups apparently have a fairly circumscribed summer range and a separate winter range at considerable distance from it. The wolves from the Byng Pass and Blue Creek areas apparently move down into the Athabaska Valley in midwinter and remain there until late April or early May.

The summer and winter ranges of this band are some 60 to 70 miles apart.

The indications are that certain packs hunt over considerably larger circuits than those already mentioned. B. White at Decoigne has remarked upon almost monthly re-appearance of wolves in his area during the winter. The wolves almost always come through Yellowhead Pass from the west and proceed down the north bank of the Miette River, keeping to the road or to the more open forest on the benches above the road. They leave the river somewhere above Giekie and strike across the higher benches to the vicinity of Pyramid Lake. From there they drop down on to Henry House Flats (Fig. 8) through a narrow cut in the escarpment wall. Where they go to from here no one knows, but somehow they get back across the interprovincial boundary within the month and continue the beat. The circuit must be at least 70 miles in length.

There is one instance of a pack of 13 or so coming up the Smoky and over Moose Pass. A pack of almost the same reported size went through Yellowhead Pass in an easterly direction a few days later and there is good reason to believe that it was the same one. The latter pack had travelled a distance of some 70 or 80 miles at the very least and probably much more.

PLATE I



FIG. 4. Summer range on Byng Pass, Jasper Park, Alta.

FIG. 5. Year-round range on Buffalo Prairie, Jasper Park.

FIG. 6. Devona winter range from the south, treeless lower slopes constitute the most heavily populated game winter range in the Parks.

FIG. 7. Close study of Devona range showing heavy overgrazing and absence of escape terrain, April, 1943.

FIG. 8. Henry House Flats winter range, Jasper Park, heavily stocked with elk and mule deer.

FIG. 9. Terracing on Devona range by bighorn, elk, and mule deer.

PLATE II



- FIG. 10. Shelter den under large boulder, Buffalo Prairie, Jasper Park.
 FIG. 11. Den in beaver lodge, Buffalo Prairie, Jasper Park.
 FIG. 12. Den on Buffalo Prairie, Jasper Park, occupied in 1945.
 FIG. 13. Rock slide used as playground by pups from den illustrated in Fig. 12.
 FIG. 14. Wolf with mange, Banff, Alta., January, 1947. Photo by U. LaCasse.
 FIG. 15. Bighorn rams far from escape terrain, on Devona range, April, 1943.

A similar monthly cycle of movement has been noted by George Camp in the Whirlpool Valley and by other wardens on other areas.

Population Controls

It will be obvious that the wolf population in the parks, inasmuch as it is little more than holding its own numerically must be suffering continual losses.

Destruction by man has taken a considerable toll of the Jasper wolves. During the four years of this study 24 wolves were shot and killed or seriously wounded by the Park wardens, 11 of them in 1944. This destruction was in furtherance of a recommendation contained in my 1943 report that limited control be applied, to the end that the population pressure within the Park not exceed that on the surrounding terrain. In Banff Park, during the same period, five adult wolves and two young pups were destroyed, while just outside the Park boundary the destruction of two dens yielded 11 pups and one adult.

As no studies have been undertaken on the provincial territory adjacent to the park it is not possible to quote figures of the approximate population of wolves there. Verbal reports from Mr. Rufe Neighbor of Entrance, Jack Hargreaves and George Wells of Jasper, and from other informed persons points to a somewhat higher concentration of wolves outside than inside the park. To this extent, then, the limited control applied by man as a supplement to natural population checks has served its purpose. Just how much influence the human control has had is problematical.

Several diseases have been reported from wolves in various parts of North America. Rabies was reported by Seton (11) and by others. Distemper has been reported by many writers on wolves particularly in the Arctic regions where domestic dogs are in widespread use in the wolf range. It may well be one of the most important diseases of this animal. Encephalitis has also been noted and proposed as an effective population control.

Sarcoptic mange has been the only disease positively identified in the wolves of Jasper and Banff Parks and it has not been at all widespread. In midwinter 1944-45, B. White of Decoigne shot an adult wolf with a serious case of mange and in September of the same year he saw another wolf that appeared to be mangy. An adult female shot at Devona by F. Burstrom in early 1946 and one of two seen on Buffalo Prairie, Jasper Park, on Dec. 18, 1946, were mangy. Coyotes in the same area exhibit a high incidence of infection with sarcoptic mange and my studies lead to the conclusion that it is the most important control upon coyote numbers. Many serious cases have been seen in adult animals but the most serious effect is upon the pups. Apparently a high proportion of the pups in both Jasper and Banff areas succumb to this disease.

In November 1946 Warden U. LaCasse of Banff Park found a shelter den 15 miles west of Banff. This was being used by a group of from seven to nine wolves. The badly decomposed carcass of a wolf lay at the entrance

to the den but its condition made determination of cause of death impossible. Another member of this band seen, and later shot (Fig. 14), on the Hillsdale meadows, 12 miles west of Banff, was badly denuded of its fur as a result of mange.

On Jan. 3, 1947, biologist E. W. Pfeiffer and Warden U. LaCasse while trailing the Hillsdale pack came upon a recently dead, frozen yearling she-wolf. It had died in a shallow den under an adjacent rock and had been dragged out by the other wolves. This wolf had 40% to 50% of its body area mangy and was extremely emaciated, weighing just 37 lb. Upon autopsy it was found that the liver bore numerous yellowish lesions scattered through the tissue, each about 4 mm. in diameter. The blood vessels of the stomach were greatly distended and the stomach and intestine contained, besides some parasitic worms, only blood, this in large quantities. This wolf had died following an internal haemorrhage but the nature of the condition leading to this could not be determined.

I have examined only five wolves for parasites. Four contained the tapeworm, *Taenia hydatigena*, one of these also harboured *Toxocara canis*, and another, adults of the granular tapeworm, *Echinococcus granulosus*. This is the tapeworm the larvae of which form the hydatid cysts common in the lungs of elk and deer in the Jasper area. *Taenia krabbei* has been taken, as a larva, from caribou and again the wolf is the logical terminal host.

Breeding

Little first hand information on breeding behaviour has been obtained during this study. The wolves are most vocal in January and February and it is assumed that this urge to sing is here, as elsewhere, an accompaniment of the early phases of the reproductive cycle. Indications are that the young are born in May and June and as the gestation period is known to be about 60 days (9) mating must take place in March and perhaps early April.

Fierce fights sometimes take place during the mating season. John Shelford of Wistaria tells me of coming upon the site of such an encounter. For many yards the ground was strewn with fur and spattered with blood. The mangled remains of a large black male testified to the fate of the vanquished. Another case of physical combat was encountered by Park Warden Frank Camp and his companions in Jasper Park in January 1946. Coming on the site of a conflict as indicated by tracks and sign on the snow they determined that four wolves had attacked a fifth, and after a vicious fight the single animal had retreated wounded. They followed and shot the animal, which was then sent to me for examination. One foot was broken and there were many surface wounds in the skin of its neck and flanks. The canine tooth of one of its adversaries had punctured the hard palate and driven deep into the nasal passages.

Two litters were discovered in the study area in 1945. About June 7, 1945, Frank Wells found a den (Fig. 12) on Buffalo Prairie, Jasper Park. The

young, apparently four in number, were active but still in the den. When the area was again visited, on June 15, the pups had left the den and were found to be hidden among the huge boulders of an adjacent rockslide (Fig. 13). Two were seen on this date and two others heard whining deeper in the slide. The pups apparently lived in and around this slide for some days as there were many scats in the vicinity and well-worn trails led here and there among the rocks or headed into the dim dry recesses deeper beneath the boulders.

In early June 1945 an Indian known as Silas discovered a wolf den on the banks of the Saskatchewan River two miles east of the Park boundary. In this instance there were five young in the den. These were dug out and destroyed.

In 1946 no dens were discovered in Jasper Park. The Buffalo Prairie den was deserted, though there were wolves in the vicinity.

Two dens were discovered in the Banff Park area in 1946. One of these was discovered by Warden Chas. Page on the bluffs overlooking the Panther River, some six miles below Windy Cabin. Mr. Page dug out this den in the last week of June and found four black pups in it. Two of these were destroyed, one eluded capture, and one was held captive until July 10, on which date we tagged and released it at the den site. The female and remaining cub were seen on the day we released the captive and there is little doubt that the family was successfully reunited.

The second den was discovered by William Winters on the bluffs overlooking the Clearwater River, five miles east (outside) of the Park boundary. This den yielded seven small pups and the female.

There are apparently many non-breeding individuals among the wolf population of the parks. Several groups upon which a careful check has been kept through three years have produced no young—or at least no young survived to join the winter hunting packs. The Willow Creek group has for three years consisted of from four to five individuals. The Brazeau River band has apparently consisted of from four to six animals constantly over the same period. The pair that wintered on the Miette sheep range from 1942 to 1945 was not accompanied by young.

The reason for this failure to reproduce is not known. It is known that female wolves do not breed until two years old and this will provide one source of non-breeding animals.

Some pups are lost to unknown causes. For example, the adult female shot at Decoigne on June 12, 1946, was given careful examination. The uterus and mammary glands gave positive evidence of this wolf having had a litter this year, but she had not been nursing for some time and had almost certainly lost her young.

Another possible explanation may be indicated by the sex distribution of the wolves destroyed in the Park during the four years. Of 25 for which record of sex has been available, 15 were males. The factors influencing sex proportions in wild animal populations are very imperfectly understood but

anything that upsets the 50 : 50 ratio in a monogamous species such as the wolf will exert profound influence upon the reproductive potential of the population. It seems to me that this, together with losses to mange and to old age, probably in large measure explains the failure of the Rocky Mountain Park wolves to increase during the three year period of this study.

Pups have been noted in three parts of Jasper Park under circumstances that suggested the presence of dens in the vicinity. They are Decoigne, Buffalo Prairie, and Honeymoon Lake. There is probably another wolf den somewhere adjacent to Hardscrabble Pass at the head of Blue Creek, where a pup was seen by Hatter on June 17, 1945, or perhaps at some point further down Blue Creek, where a pup was shot by Warden Jones in October, 1946.

Dens

The Saskatchewan River den as described to me by its Indian discoverer was dug into the sandy marl of a knoll adjacent to the river. It had a depth of about 10 ft. but further details were unobtainable.

In mid April, 1945, Frank Wells found what appeared to be the beginnings of a den on Buffalo Prairie. Here an ancient beaver house, about 8 ft. in diameter, left dry by the breaking of the dam, had been opened at both ends (Fig. 11).

When it was examined by me on May 4 it showed signs of recent excavation, and there were fresh wolf tracks in the mounds of loose earth at the tunnel entrances. The burrows were 18 in. in diameter and approximately circular. This den was not used after our visit and the later discovery of an occupied den about a half mile away suggests that the beaver house site was never intended for such use.

The Buffalo Prairie den discovered by Frank Wells in early June 1945 was in an almost ideal location (Fig. 12). A number of huge boulders resting partly buried near the crest of a rocky ridge elevated some 60 or 70 ft. about the general level of the surrounding country and sparsely timbered, constituted the den site. The den itself was entered down a short slope between two large rocks and then a tunnel measuring 16 in. high by 18 in. wide had been excavated under the largest of the boulders. It led back about 7 ft. into a dry, slightly enlarged chamber that apparently served as the nest, although no bedding of any sort was present. A few feet away was another burrow under a large rock, apparently used at one time as a den but more recently as a shelter. Fifty feet away, on an aspen covered slope, a chamber (Fig. 10) large enough to accommodate two or three adult wolves in shelter and dryness had been dug under another large boulder.

A rock slide, composed of the debris from a 100 ft. cliff offered shelter and a playground for the pups among the large rocks heaped in disorder.

A fine clear spring emerged from the ground not 15 yd. from the den.

Remains of prey animals representing several years of habitation were strewn about the vicinity.

The Panther River den found by Warden Chas. Page in June 1946 was situated on the side of a small depression in the summit of a ridge bordering the river. The den was about 12 ft. in length and instead of penetrating straight into the hill it paralleled it after reaching a depth of about 5 ft.

A search of the area adjacent to this den led to the discovery of four other dens in fair state of repair and six others, much older and now caved in. All but one of these were near the crest of the 30 to 40 ft. bluff that borders the river course and had a broad view up and down the valley. Characteristically the dens had two entrances, a few feet apart and converging on the main tunnel some six feet from the entrance. These entrance tunnels were large enough to permit me to enter in a prone position.

At Hillsdale in Banff Park in January, 1947, a pack of five wolves was using a group of blown down pines, with their needles still on, as a shelter. Into this den they had carried quantities of elk hair, possibly attached to chunks of meat used for food.

Territorial Defense

Twice, in May and early June 1945, prior to his discovery of the Buffalo Prairie den, Park Warden Frank Wells had his dogs molested by wolves. On May 24 he, with his three dogs, two cougar hounds, and a black-and-white collie mongrel, were proceeding across country two or three miles from the den when three wolves began to circle the group, howling as they did so. Wells finally shot and wounded one wolf and, as his collie ran in, the wolf locked jaws with it, tearing out one of the dog's upper molars. The wolf escaped. A few days later, while he was riding through the area with his dogs, a large black wolf rushed from cover and seized the collie, first by the throat and then by the small of the back, inflicting deep wounds. Wells rushed to the rescue of the dog and the wolf left, then as he bent over the injured and apparently dead dog, he became aware that the wolf was closing in on the run. By shouting and waving his arms Wells checked the animal's rush while it was still a few feet distant and it then made off into the timber. The dog lived.

The circumstances do not seem to indicate that the wolf was knowingly attacking a man. It was aroused to a killing frenzy and the man was half hidden from its view and probably unrecognizable.

Relations with Other Carnivores

There has been little opportunity of gathering data on this aspect of wolf biology. Little sign of active hostility between wolves and coyotes has been seen, though the latter are normally present as scavengers at any meal the wolves provide for themselves. In December 1943 F. Burstrom at Devona found where four wolves had caught and killed a coyote and torn it to pieces. In the same region in August 1945 he saw five coyotes following a large black wolf. The wolf paid little attention to the coyotes except to threaten any

that came too close. Near Jasper in December 1946 J. Hatter noted that coyotes were almost always present in the vicinity of the wolves. According to figures supplied me by men who have hunted both animals from an automobile on the ice of Ootsa Lake, B.C., the wolf at its best seldom attains a speed greater than 25 miles per hour while the top speed of a coyote is almost 10 miles an hour faster. This being the case the coyote is well equipped, under ordinary circumstances, to stay out of reach of the wolf.

Present indications are, then, that wolf-coyote interaction is largely beneficial to the coyote through carrion made available at kills not completely consumed by the wolves.

The grizzly bears of Jasper Park are, unlike those of other parts of the Rocky Mountain Parks, actively predaceous and subsist to an important degree upon elk and moose run down and killed by themselves. Grizzlies normally feed for several days upon such a kill and cover the remains beneath a pile of debris at the end of each meal. Where wolves are not present the bear frequently does not remain in the near vicinity of its kill between meals. However, in the autumn, if wolves are present and in hunting packs, the bears change their behaviour and bed down close to any kill they make. This behaviour has been noted by several wardens and evidence of it has been seen by myself. In three such instances the bear had made its bed close up against the partially eaten and buried carcass. Frank Wells, in the autumn of 1944, came upon one large grizzly as it lay spread-eagled upon the top of the buried carcass of a large bull elk.

Tracks have, in several instances, revealed where wolves had circled about a bear defending its kill but no attempt had been made to molest the animal.

In conversations with several guides that take hunting parties into the region north of Jasper Park several accounts have been heard of wolves molesting grizzlies; none of these was told to me by the viewers and they were accepted with reservations. One guide even went so far as to state his opinion that (in certain areas) the grizzlies are so constantly harried by wolves that they forsake the regions for others containing fewer wolves. No factual basis for such an opinion has been advanced by anyone.

Hunting Behaviour

Much has been written concerning the hunting behaviour of wolves in various parts of the country. The best accounts are those given by Murie (9) in his study of the wolves of Mount McKinley. Observations made during the present study confirm those of other authors. The usual winter hunting pack consists of from four to seven individuals, with five or six the most frequent numbers. Packs of 10 or a dozen have been reported once or twice in the Jasper area. The largest group recorded was believed to contain 14 individuals.

While travelling in the snow over ridges or other unpromising game country, or when merely travelling, the wolves in this area characteristically travel

single file, the leader breaking trail and the others treading in the same tracks. Then, upon entering a swamp, swale, or thicket, the pack changes to the hunting order, which is line abreast. In this region, where much of the hunting is done in timbered country with restricted visibility, the line abreast hunting pattern enables the pack to sweep a wider band. When game is jumped the wolves are often in a position to outflank the animals and to effect speedy capture.

In the Hillsdale area of Banff Park, there is much abruptly rolling country with steep sidehills and sharp ridge tops. Here, in January 1947, with 18 in. of snow on the ground, the wolves were running the ridge tops until the elk were spotted on the slope below them. A quick downhill rush and simultaneous attack by several wolves was almost always successful in an immediate kill.

At Patricia Lake on Dec. 24, 1946, five wolves had jumped a three year old bull elk from its bed in a willow swale. They drew blood within 20 yd. and killed the beast before it had run 120 yd.

During the summer wolves frequently hunt alone or in smaller groups and a lone wolf is capable of pulling down the largest of the game animals at present occurring in the Rocky Mountains. Several instances of single wolves killing moose and elk were noted.

Several kills involving elk were examined in the spring of 1943 and 1944, and in the winter of 1945. Most of these had not been hamstrung nor had they been pulled down by the throat. In each instance the attack had been from the rear and side with the wolf seizing the flank at the point where the leg joins the abdomen. A wound here lets the viscera out, with the opening of large blood vessels and reasonably rapid death.

One adult cow elk pulled down near Decoigne in April 1943 was examined carefully by B. White who could find no wounds but a small tear in the left flank. The single wolf responsible for this kill had eaten a few pounds of flesh from the udder and upper leg and did not return to the carcass—possibly because of human interference.

An adult bull elk examined on Apr. 20, 1943, near Decoigne, had been killed by six wolves. After a short run this animal had been overtaken and pulled down. The nose, throat, and flanks were torn. A young bull elk examined on Apr. 23, 1943, at Mile 38 on the Banff-Jasper Highway had likewise been seized by the throat.

No instance of hamstringing has yet been seen or reported to me.

Long pursuits are unusual in the Rocky Mountain region, probably because the varied terrain usually permits a quick termination of the chase one way or another. The longest chase we have noted was at Pyramid Lake in December, 1945. Here a small pack ran a yearling elk about a mile and a half before killing. Blood showed on the snow for the last quarter mile.

Contrary to the opinion of many people the wolf is by no means always successful in capturing the object of its chase. As already stated, the wolf's

top speed under optimum conditions is only in the vicinity of 25 miles per hour. I have clocked running speeds of moose at 27 miles per hour, elk at 28 and 29, a buck mule deer running its best on rough ground alongside the highway reached a top speed of 30 miles an hour and averaged 28 miles per hour for about a quarter of a mile, by the end of which it was tiring quickly.

It will thus be seen that the ungulates can, over short distances at least, outrun a wolf. The defence technique most frequently resorted to by elk, moose, and mule deer when pursued by wolves is to make for the nearest water and take refuge in it. The wolves will not enter in pursuit. On several occasions single deer, elk, and moose have been seen making use of this defensive behaviour and Frank Wells tells me he has seen as many as 35 elk in a group standing in the Athabaska River.

A two year old cow moose, seen by picnickers on Aug. 24, 1943, was being closely pursued by four wolves. It beat the wolves to the Miette River, plunged in, and crossed over. The presence of people with a dog caused the wolves to drop the chase, but it is probable that the moose had already made good its escape. On the Smoky River in January 1946, Park Warden McGuire noted that three wolves had made several unsuccessful attempts to catch moose. Hampered by the deep snow, the wolves failed and later returned down river to areas where the snow was shallower.

In October, 1944, at Decoigne, a cow elk pursued by wolves made the river but died there as a result of flank wounds received during the chase. Warden White reports that the wolves made no effort to reach the carcass but left it to decompose. Frank Wells has noted three similar instances in his area.

Even the water refuge can be a not unmixed blessing under certain circumstances. In the late autumn, when water temperatures are close to the freezing point, deer and elk taking refuge in the open water of rivers not infrequently become so chilled that they collapse into the water and are drowned. No such instances were seen by me but several wardens gave first hand accounts of such events.

Occasionally an animal pursued by wolves will come to bay and beat off its pursuers. Such an instance was noted by F. Wells during the winter of 1944-45. Tracks revealed that a band of about seven wolves ran a cow elk down the bank of the Athabaska River above the falls. At the falls, where the river plunges deep into a short canyon, the elk came to bay on a narrow promontory that gave her protection at her flanks and back. The wolves after a bit of skirmishing gave up the chase and went in search of other prey.

In November 1945, Warden Aleck Nelles at Snaring Station followed three wolves and found where they had attacked a moose. The animal, instead of running, had turned at bay and, by striking with its forefeet, had successfully beaten off the wolves. Shortly after leaving the moose the wolves killed a deer.

In soft snow wolves are often at a disadvantage and under such circumstances Warden R. Jones has seen signs of many abortive chases after deer in the Willow Creek area.

When snow of a foot and a half or more in depth develops a heavy crust the advantage is reversed and wolves can kill deer practically at will.

Another hunting technique used in some instances is that of running game out onto the ice of frozen lakes and streams. Under slippery ice conditions ungulates are with difficulty able to run and not infrequently lose their footing and their lives.

An occasional animal, hotly pursued by wolves plunges to its death over a cliff or into a canyon. An elk and a moose died in this way in the winter of 1944-45 on the Red Pass road as a result of plunges into rock cuts on the old railroad right of way. Such instances are probably more accidental than purposeful.

When hunting small game, such as rabbits, the wolves usually move at a walk in what appear to be aimless wanderings. I saw no sign of an effort on the part of the wolves to track down the rabbit—rather the mode of hunting seemed to be designed to flush the animal by chance and to catch it in a swift rush.

I was not able to observe the technique used in hunting ground squirrels and marmots but it probably does not differ greatly from that used by coyotes in search of the same prey.

Food Consumption and Caching

It has been difficult to obtain information upon the frequency with which wolves make kills. The nomadic behaviour of the creatures makes it most difficult to determine this important element in wolf behaviour.

Under favourable local conditions, at Jasper, and at Hillsdale in Banff Park, in December 1946, and early in January 1947, biologist E. W. Pfeiffer, accompanied by Warden F. A. Bryant in Jasper, and U. LaCasse in Banff, was able to determine the frequency of kills for two separate packs of five or six wolves. Each of these groups was killing and consuming three elk in a two week period with indications that two small elk might be taken in a week. At this rate the wolves were accounting for from one to one and one-half elk per wolf per month in the midwinter months.

Wolves can at times consume large quantities of meat. At Hillsdale, Banff Park, on Jan. 7, 1947, five wolves killed and ate an entire calf elk. On or about Jan. 1 this pack had killed a cow elk and in two days had eaten the greater part of it.

Behaviour at this kill was characteristic of many others. After eating their fill the wolves retired a few yards to a knoll, there each animal dug a circular bed down to the pine needles, usually at the base of a tree. The bedding area was much padded down and strewn with faeces and indicated that the wolves had moved little until the greater part of the elk was eaten.

In March 1943 four wolves killed a mule deer doe near Devona and in about four hours stripped the greater part of the flesh from it.

In November 1943 Warden R. Jones came upon a young buck deer so recently killed as to be still warm and yet the five or six wolves in the pack had already removed most of the flesh.

On Nov. 1, 1942 Warden R. Jones came upon a group of half a dozen or so wolves feeding upon an adult buck mule deer. Back tracking the pack he came to the warm remains of a fawn. On the other hand there are the many times when wolves have travelled the trail for two or three days without any apparent kill.

In November 1945 three wolves at Snaring unsuccessfully attacked a moose and later killed and ate two mule deer and a calf elk all in five days.

F. Wells during a winter trip up the Snaring had occasion to follow the trail of a wolf pack of about six individuals. They killed two moose in three days eating only part of each.

The assumption that in each of the above instances the wolves ate all the flesh is probably erroneous. It is well known that wolves frequently will carry away large chunks of meat after they have fed to repletion. F. Wells, who has followed wolves with his dogs, informs me that quite frequently the dogs dig up meat cached by the wolves. Such caches were usually in some old mossy log. The meat was buried in shallow holes dug for the purpose. At other times it was merely buried in snow.

In November 1943 Warden R. Jones noted where five wolves had killed a deer near Topaz Lake. After feeding on the carcass they carried large chunks of meat to a nearby knoll where they buried them in the snow.

When hunting for den-bound pups the wolves have been known to carry home such large objects as the head and antlers of a seven point bull elk. At the Buffalo Prairie den on July 6, 1945, I counted the following animal remains—skulls of a yearling mule deer, a senile cow elk, two calf elk, an adult cow elk, a seven point bull with antlers on, part of another calf elk, and the right fore leg of an adult elk, the right hind leg and entire rib basket of a yearling elk, the left fore legs of a yearling, a two year old and an adult elk, both hind legs of another elk, the right hind leg of a yearling elk, the right front and left hind legs of a mule deer, and a beaver skull. When the den was visited two weeks earlier there were remains of a lamb sheep, consisting of almost the entire vertebral column.

At the Panther River den, when I examined it on July 10, 1946, there were few remains of prey animals. A beaver skull, parts of the fore limb of a deer and bones of a young cow elk, apparently killed right beside the den, were the remains present. The pups at this den were six weeks to two months old and had apparently been fed largely upon the flesh of large ungulates and upon mice. This pair probably stripped the flesh from the bones of their prey and brought home pieces of meat and hide. There was an adult cow elk kill about 300 yd. from the den and the cubs with their mother were feeding on this when they were first seen.

Wolves have the very dog-like habit of sometimes carrying an old bone with them. It is a fairly frequent experience among those who have followed the

tracks of wolves, to have the wolf drop some old and meatless bone that it had apparently carried for several miles.

When feeding on a carcass wolves may or may not break and consume the long bones. If the prey is a young animal the leg bones and skull are usually eaten, except for the hardest parts, such as the teeth and the epiphyses of the long bones. The heavier bones of elk, moose, and adult bighorn rams are apparently beyond the power of the wolf to crack them. Even where game abounds one frequently finds quantities of dried leg skin and tendons in the scats. These indigestible items must be obtained from old and dehydrated carcasses.

Food Habits

Data upon the food habits of the wolves of Jasper and Banff Parks has been obtained from two main sources, the analysis of scats and the observation of kills definitely attributable to wolves.

The data obtained from the examination of kills is almost inevitably confined to the big game species. The smaller food items are consumed in their entirety. For this reason it is not possible to obtain an accurate picture of the diet of the wolves by this means alone.

Scat analysis has been widely used as a method of obtaining quantitative data upon the food habits of animals. Where the sample of scats obtained is unbiased as to source this method probably gives a fairly accurate representation of the actual diet. It is, however, most difficult to obtain a truly representative sample.

During the winter months the wolves often travel the park trails and leave scats where they are easily found. In the summer this is true to a much smaller degree. Particularly is this true of the wolves that repair to the alplands in the summer. Scats are left far and wide over the mountains and one finds few, even by diligent and painstaking search.

The winter scats so far obtained for the purpose of this study are probably fairly representative. The greater part of the winter scats are from the Snake Indian, Miette, and Panther river valleys, where the various big game species are present in approximately the same proportion that they are on the winter ranges in general throughout the park. Winter scats outnumber those representative of the summer season and inasmuch as the summer diet is apparently higher in the proportion of rodents eaten and correspondingly lower in game items it can be expected that additional data from the alpland regions particularly will change the proportion of rodents in the annual diet.

Half of the summer scats so far collected are from the Buffalo Prairie den. This is situated in one of the best beaver districts in Jasper Park, an area that is now deteriorating as a beaver habitat as a result of long-continued overpopulation, with consequent destruction of food trees. The beavers are, as a result, more vulnerable to predation than under average conditions.

In order to appraise the degree of selection undertaken by the wolves, or the ability of the various species of game to escape the assaults of wolves, it is

TABLE I
FOOD HABITS OF WOLVES AS REPRESENTED IN 420 SCATS FROM JASPER
AND BANFF NATIONAL PARKS

Food items	Occurrences in winter scats		Occurrences in summer scats		Occurrences in annual diet	
	No.	%	No.	%	No.	%
Elk, <i>Cervus canadensis</i>	149	49	62	42	211	47
Mule deer, <i>Odocoileus hemionus</i>	46	15	20	14	66	15
Moose, <i>Alces americana</i>	26	9	6	4	32	7
Bighorn, <i>Ovis canadensis</i>	19	6	11	8	30	7
Caribou, <i>Rangifer arcticus</i>	14	5	1	0.5	15	3
Goat, <i>Oreamnos americanus</i>	2	0.5	0	0	2	0.5
Horse, <i>Equus caballus</i>	2	0.5	0	0	2	0.5
Total ungulates	258	85	100	69	358	80
Snowshoe hare, <i>Lepus americanus</i>	30	10	2	1	32	7
Beaver, <i>Castor canadensis</i>	5	1.5	25	17	30	7
Porcupine, <i>Erethizon dorsatum</i>	5	1.5	1	0.5	6	1
Ground squirrel, <i>Citellus columbianus</i>	0	0	6	4	6	1
Marmot, <i>Marmota caligata</i>	0	0	1	0.5	1	Trace
Vole, <i>Microtus</i> sp.	3	1	7	5	10	2
Coyote, <i>Canis latrans</i>	0	0	1	0.5	1	Trace
Deer mouse, <i>Peromyscus maniculatus</i>	0	0	1	0.5	1	Trace
Mantled ground squirrel, <i>Citellus lateralis</i>	0	0	1	0.5	1	Trace
Total rodents, etc.	43	14	45	32	88	18
Berries	1	Trace	1	0.5	2	0.5
Grass and sedge	2	0.5	—	—	2	0.5
Total item occurrences	304		146		450	

pertinent to attempt to determine the relative abundance of each species on the wolf range.

The only basis for this comparison lies in the total of animals seen on the general areas from which the wolf scats were collected. No special effort was made to find any one particular species and it is thought that the figures approximate the relative abundance of the six species of big game available to the wolves in Jasper Park except in the case of bighorn, which, by reason of their superior visibility, are possibly somewhat biased on this count.

In 1941 and 1943 game seen was as follows: Bighorn, 2251; elk, 1721; mule deer, 595; goat, 458; moose, 156; caribou, 36. The relative abundance of these species calculated from the above figures is given in Table II.

It will be noted that in several respects contribution to the annual diet is not strictly related to relative abundance. In comparison with the number of kills recorded, deer apparently contribute to the diet in greater proportion than they are represented in the population. For example, while only about one-third as many deer as elk were seen, deer kills were about half as numerous as elk kills.

While elk, deer, and moose appear in the diet in fairly close relation to their relative abundance it is apparent that sheep and goat are in another category.

TABLE II

CLASSIFICATION OF WOLF KILLS IN JASPER AND BANFF PARKS AND COMPARISON OF SCAT ANALYSIS AND RELATIVE ABUNDANCE OF GAME SPECIES

Species	Number of kills	Percentage of total kills	Percentage of item in scats containing game	Relative abundance of prey species, %*
Elk, <i>Cervus canadensis</i>	64	54	59	33
Deer, <i>Odocoileus hemionus</i>	27	23	18	11
Moose, <i>Alces americana</i>	14	12	9	4
Bighorn, <i>Ovis canadensis</i>	10	9	9	42
Caribou, <i>Rangifer arcticus</i>	2	2	4	1
Goat, <i>Oreamnos americanus</i>	1	1	Trace	9
	118			

* Based upon total counts of game seen during 1941 (1) and 1943 (2).

They are apparently better equipped to escape the wolves than are the forest game species—or are hunted to less degree under the ecological conditions obtaining.

On the basis of present data the game species comprise 80% of the annual diet, while another 18% is supplied by the rodents. These percentages are similar to those determined by Murie (9) for the annual diet of the Mount McKinley Park wolves. In that instance game comprised 69% and rodents 27%.

On a seasonal basis the winter diet in the Rocky Mountains consisted of game 85% and rodents 14% whereas the summer diet was game 69%, rodents 32%. This reflects the greater availability of rodents during the summer, when the hibernatory species are active and the beavers are leaving their pond retreats in search of food.

Berries and grass have taken an unimportant part in the scats so far examined.

If the percentage composition of that part of the diet consisting of big game (358 items) is compared with the proportion of the various species of big game in the 118 wolf kills recorded there is remarkably close correlation indicated. This comparison is made on Table II. It will be noted that the various species occur in the same order of importance in both bodies of data and that the individual percentages are of corresponding orders of magnitude in most instances. This correspondence serves to reinforce the probability that the general pattern of food preference is reliably indicated in the present data.

Discussion of Food Items

Elk, Cervus canadensis nelsoni

The wolf range in Jasper and Banff Park is heavily populated with elk. In Jasper Park it is not possible to make an accurate census of the total elk population but it is probably not less than 3000 head. The winter range is,

much of it, heavily overpopulated. Range conditions have deteriorated drastically (Figs. 7, 8, 9) and the reproductive rate has dropped until in December 1944 the calves numbered only 18% of the cows of yearling age and over.

The greater bulk of an individual elk, from two to three times that of a mule deer, when taken with reference to percentage occurrence in the scats, indicates that on the basis of present scat data elk are apparently being subjected to smaller proportional loss than are the deer. It should be mentioned that several bands of wolves, notably those at Decoigne, Athabaska Falls, and the Whirlpool are, according to field observations of the district wardens, subsisting almost exclusively on elk. Deer do not winter on these wolf ranges. Very few scats from these places are included among the sample analysed. For this reason it is believed that the actual kill of elk and its proportionate contribution to the annual diet is greater than indicated by present data.

In summer scats calf elk is represented in equal proportion with adult remains, a fact that reflects a relatively high take of the calves.

*Mule deer, *Odocoileus hemionus hemionus**

Deer remains appeared in 66 scats and represent 15% of the annual diet. In a comparison of the game items alone, deer represents 18% of the annual diet. Inasmuch as 595 mule deer were tallied as against 1720 elk, it is probable that deer were one-third as abundant as elk in the wolf environment. On the other hand, on the basis of kills found, these two were contributing closer to the ratio of 1 to 2. It must be remembered also that one deer probably appears in no more than half as many scats as an elk. The inference is, then, that deer have been selectively hunted by the wolves.

It is not possible to estimate the total population of mule deer in Jasper Park, but in certain parts of the winter range the density is high. For example, several counts on the Devona winter ranges in May, 1943 and 1944, have yielded population figures of from 60 to 68 deer per sq. mile. In the vicinity of Jasper and of Henry House the winter population is estimated at 17 per sq. mile, whereas the marginal winter range at Willow Creek in May 1944, had five deer per sq. mile.

Another important factor involved in the preying of wolves upon deer is the physical condition of the deer. The seriously overgrazed winter ranges of the Athabaska Valley of Jasper Park do not offer an adequate supply of the most preferred deer food-plants, and as a result the fawns have difficulty in maintaining their condition and many die. Even so there are indications that predator pressure is not removing all the seriously weakened animals. In April and May of each year I have found several senile deer so weakened from parasite infestation and malnutrition that they were incapable of running. These animals would certainly have been eliminated had the predator pressure been heavy.

Moose, Alces americana americana

Moose remains appeared in 32 scats, 7% of the total sample. Thus on the basis of the scat analysis as also on the basis of the numbers of known wolf kills moose constitutes the third item in importance in the annual diet, while it is fifth in abundance in the total game population. This is in contrast with conditions reported from the Mount McKinley district of Alaska, where wolves seldom bothered moose.

Summer occurrences of moose are all those of moose calf remains. While it is certain that some calves are killed by the wolves, it should be borne in mind that the losses of moose calves to accidents are perhaps higher than similar losses in any other local species of big game. Carrion may well make up a fair part of the calf moose item. More than half of the occurrences of moose in winter scats also consist of calf remains.

Bighorn, Ovis canadensis canadensis

In view of the abundance of bighorn in the park and their apparent vulnerability to predation the small number of scats containing this animal is surprising.

On the Devona ranges large bands of bighorn graze upon the open grassy benches far removed from any terrain offering natural protection (Fig. 15). The behaviour of these sheep certainly leaves one with the impression that wolves occupy an unimportant place in their lives. Few wolf kills have been found on this area, though wolves have been present every year.

Most of the other sheep ranges of the park offer good grazing closely adjacent to rocky bluffs and cliffs where sheep could escape from wolves. On Dec. 26, 1944, James Hatter, assisting in this study, hiked from Devona to the Miette winter ranges. Sheep were much in evidence grazing on the grassy benches. The following morning no sheep were to be seen on these grasslands, they had all taken to the rocks. Hatter found a pair of wolves prowling in the vicinity. In the same area in May 1945 wolves were still present and the remains of two sheep may have represented successful hunting on their part. Though I searched the area thoroughly only these two sheep kills were discovered, along with the remains of one elk and a deer. The local sheep population varies from 100 or so to four or five times that number, in response to snow conditions at higher elevations.

It is noteworthy that the sheep on this range were wilder than on any other.

On Buffalo Prairie, where one occupied den was located and where wolves ranged through the year, the bighorn were ranging the low forested ridges (Fig. 5), feeding on the open, westfacing sidehills but crossing through the timbered valleys from one ridge to the next. As sheep range it is of a very low order with sparse food supply and few natural protective features save scattered small cliffs and rockslides and yet the sheep are apparently holding their own there. Their reproductive success is, however, lower than that of any other band. In December 1944 this flock was found to have a proportion of lambs to ewes of 10%, while the other flocks of the Athabaska Valley

averaged 45%. The part played in this by the wolves is unknown. Coyotes were present in some numbers and mountain lions killed an occasional sheep.

Between Dec. 21 and 31, 1945, J. Hatter studied a group of five grey wolves working the northern end of Buffalo Prairie. A band of 10 bighorn (two rams, six ewes, two lambs) were frequenting Old Fort Point, a place offering excellent escape terrain close to a small feeding area. The wolves worked the point at about three-day intervals covering it thoroughly at each visit. Repeated census of the sheep revealed almost certainly that one of the lambs was taken during the 10 days.

In November 1944, F. Wells found an old ram that had been killed by wolves as it was crossing from Buffalo Prairie to the west side of the Athabaska River. Caught out on the timbered flats it must have fallen an easy victim. Remains of a lamb were found at the Buffalo Prairie den by Wells on his first visit to it. In other flocks near Jasper sheep were dying of old age during the winter. Two such senile rams came down from the slopes of the Palisades to die on Henry House Flats. This is an area regularly traversed by wolves.

The evidence seems to indicate that the Jasper Park wolves seldom hunt sheep, that the animals taken are those from time to time surprised away from escape facilities. However, the condition on the Buffalo Prairie area with regard to sheep is that the population is kept to a point of bare survival. From the National Park standpoint this is unimportant but from a game production standpoint this marginal sheep terrain might be made to produce a shootable surplus in the absence of wolves while in their presence it probably could not.

Caribou, Rangifer arcticus montanus

Little has been learned regarding the circumstances surrounding wolf predation upon caribou in the mountainous terrain of Jasper Park. Warden R. Jones of the Blue Creek area has seen evidence that wolves were pursuing caribou while these animals were wintering in the forested country between Blue Creek and Willow Creek. It is from this area that the scats containing caribou remains came. This animal occurred in 15 scats representing 3% of the annual diet.

Goat, Oreamnos americanus columbae

The preferred terrain of goats seems to render them almost immune to attack by wolves. One kill discovered by Warden F. Burstrom in December 1945 was a young animal caught crossing from one range to another. By frequenting the goat licks in the summer time wolves could quite easily find opportunity of attacking goats. At such locations, as, for instance, the Shalebanks lick on the Snake Indian River, large numbers of goats pass through dense timber for more than two miles while going and coming between their mountain-top feeding grounds and the lick. Bears occasionally kill goats at this and other similar licks.

Snowshoe hare, Lepus americanus americanus

The snowshoe hare, or rabbit, is quite common locally in the Athabaska Valley but there has been no irruptive increase since 1915. Coyotes hunt the animals as an important part of their diet (5). In the Devona-Miette area, where rabbits are as common as they are anywhere in the park, 32 scats taken in 1944-46 contained this animal.

Beaver, Castor canadensis canadensis

In certain areas beavers are an important dietary item. For instance 25 out of 60 of the pup scats at the Buffalo Prairie den consisted entirely of beaver remains. Here beaver exceeded in importance deer and elk combined.

In 1930 the Athabaska Valley of Jasper Park was superlative beaver range and bore a very heavy population despite the abundance of predatory animals. The removal of trees by these beavers at the time when the elk and moose were eliminating all seedling trees has had the inevitable result of rendering large areas of the park unsuitable for beaver.

As stated above, Buffalo Prairie has for a long time been noted for the density of its beaver population. The many streams that wind between the rugged hills and ridges are a succession of old beaver meadows and dams in various stages of disrepair. There are still several active colonies, but the aspens, the favourite beaver food, have been killed to such an extent that certain beaver colonies are subsisting on jack pine. Others are wandering many yards from the ponds in search of food. These circumstances render the beavers easy prey to wolves, coyotes, and bears. There is little doubt that wolves and other predators are effective in reducing a beaver population that has eaten itself out. In this area the beavers have worked progressively further and further up small streams, so that when the last food is eaten they cannot find safe passage to a large river or lake. Many of the streams here are so small that they offer little protection to migrating beaver.

I have seen no evidence that predators can prevent a beaver population from increasing until it is so large that safely available food becomes inadequate.

Porcupine, Erethizon dorsatum nigrescens

Six scats contained porcupine remains, including some heavy quills. It is not known how wolves manage to kill porcupines without themselves receiving crippling loads of quills. Murie (9) describes an ingenious technique used by a husky dog in killing porcupines. It consisted essentially of seizing the animal by the nose and killing it with a bite through the head. Wolves apparently skin out the porcupine by opening it from the ventral surface.

Ground squirrel, Citellus columbianus columbianus

These animals are hunted by wolves to a certain extent during the summer months. At lower elevations these animals come out of hibernation in late April and some remain active above timber line until early September. During this time they figure importantly in the diet of coyotes. So far few

wolf scats have been picked up on areas frequented by ground squirrels and it is possible that the 2% dietary item provided by this animal would be increased by further study.

Marmot, Marmota caligata oxytona

Marmots have not been common, during this study, on the parts of the alplands frequented by wolves and they are apparently not much hunted under existing circumstances. Just one scat contained marmot remains.

Mice

The microtines have been scarce during the period covered by this study, but, even so, coyote scats have contained their remains in appreciable numbers. Wolves apparently do not bother to hunt such small fry. Mouse remains occurred in seven summer and three winter scats.

Culling Effects

It will be understood that it is often most difficult to determine from the remains of a wolf kill whether or not the animal eaten had been in good or poor physical condition. Age class can frequently be determined and serve as indicative of presumed vitality and sometimes the remains may be fresh enough to permit determination of nutritional condition by means of an examination of the bone marrow.

It is inevitable, however, that the circumstances preceding the deaths of many wolf-killed animals remain unknown.

In an attempt to determine to what extent the wolves were preying upon cull classes rather than upon animals in the prime of life, all kills for which age or condition or both were determinable have been classified into three categories, namely, animals under one year, animals over one year but not senile or otherwise ailing or injured, and animals senile, diseased, or injured. In these groups are included all dead animals found, no matter what the cause of death. Because of the easily destructible nature of the skeleton, mule deer did not lend themselves to this classification; fawns were easily recognized but my figures for the other two age groups were biased by the number that had to be discarded as unclassifiable.

Elk and bighorn are particularly suitable for treatment and an examination of the data for these species reveals some interesting facts. Of 66 elk carcasses examined, 20 fell into the very young group, 29 into the mature category, and 17 were diseased or senile. In this species, then, it appears that almost as many animals are dying in the prime years of life as in the other two age groups combined. Actually, deaths during the first year greatly outnumber those in any other age group but the young animals are almost completely consumed by predators or scavengers and consequently leave few or no remains to be discovered. It is incontrovertible, however, that the mature category is contributing to a greater degree than would be expected if the losses were confined largely to the cull classes.

It should be mentioned here that the elk of Jasper Park are quite extensively infested with the lungworm *Dictyocaulus viviparus* and with the hydatid cysts of *Echinococcus granulosus*. The former is probably unimportant in mature, otherwise healthy elk, but the latter is known to have a readily discernible effect on the physical condition of infested hosts. The pulmonary situation of these cysts in elk might be expected to interfere still further with the ability of the infested animals to avoid wolf pursuit.

A certain proportion of the prime age group appearing as kills may owe its presence to this disease, which is not detectable from examination of the remains of a kill.

It has been shown elsewhere that the survival of calves is no greater on the wolf-free than upon the wolf-inhabited areas. There is thus no evidence that the wolves are selectively removing the young of elk.

The situation with regard to predation upon bighorn sheep is different. In this species the majority of the remains discovered have been in the old or ailing group and it has been shown elsewhere that the percentile losses of sheep during the first year are lower than for almost any other species. From this it can be deduced, either that wolves play so unimportant a role in the life equation of sheep that their kills do not alter the normal loss pattern appreciably, or that wolf predation upon sheep is, in large measure, on the cull classes. Field evidence favours the latter interpretation.

It is pertinent to emphasize that quite apart from the culling effect, it has been abundantly shown, by Errington (4) and others, that predation upon excess populations is relatively high. At current population levels perhaps half the elk in Jasper Park, and but little less in Banff Park, are surplus population.

Influence of Wolves on Sex Ratios and on Survival of Young Game

The successful analysis of predator-prey interaction is predicated largely upon a thorough understanding of the food habits of the predator and ecological circumstances that permit a direct approach to the problem of determining the net influence of the predator upon the prey. The presence of wolves over most of Jasper Park and their virtual absence from most of Banff, Kootenay, and Yoho Parks, while the other predatory species are fairly evenly distributed, offers such an opportunity of assessing the net effect of wolf predation upon big game stocks.

Data for use in this study were obtained by extensive vital statistics tallies of game herds in all parts of the Rocky Mountain Parks from 1943 to 1946. The totals available are much lower than the total counts of game seen because only those counts have been selected in which certain identification of the various sex and age groups was possible. These data were then segregated into groups based upon the presence or absence of wolves in the areas. The results are set forth in Table III.

TABLE III

COMPARISON OF SEX RATIOS IN ADULT POPULATION AND SURVIVAL OF YOUNG ON WOLF-INHABITED AND WOLF-FREE AREAS

Species	Wolf-inhabited areas						Wolf-free areas					
	Males		Females		Yearlings		Males		Females		Yearlings	
	No.	%	No.	%	No.	%*	No.	%	No.	%	No.	%
Elk	189	25	556	75	99	18	319	21	1168	79	296	25
Moose	105	64	60	36	13	22	102	60	69	40	16	23
Deer	152	34	291	66	90	31	78	36	140	64	35	25
Sheep	365	44	468	56	163	35	273	45	344	55	102	30

* Expressed as a percentage of females over one year of age.

It will be apparent from these data that there is a very close correspondence in the figures derived from the wolf-inhabited and the wolf-free areas. The survival of young elk to yearling age on the areas without wolves appears to be higher than it is on the areas hunted by wolves (25% as against 18%). However, figures taken from the spring census of elk in the Bow Valley made by H. U. Green in 1945 reveal that in this wolf-free area in an aggregate count of 1029 elk the percentage ratio of yearlings to females over one year was 19. This is virtually identical with the percentage on the wolf run areas of Jasper Park.

The slightly higher survival of fawn deer and lamb sheep to yearling age on the wolf-inhabited areas may or may not be significant, but it is difficult to avoid the conclusion that under the circumstances prevailing at present in the Rocky Mountains, circumstances that feature overcapacity game stock and badly depleted ranges, the wolves are not the critical factor influencing the survival of the young deer, sheep, moose, and elk to yearling age. Other studies I have undertaken in these parks (2 and 3) have made it most obvious that the critical limiting factor is range conditions. The comparative figures from wolf-inhabited and wolf-free areas reveal that at the present population levels of wolves and ungulates the net effect of wolves on game herd productivity in Banff and Jasper Parks is inconsequential. It is apparent, then, that evidence points to the wolf as being of lesser importance to the survival of game in the parks than are the welfare factors, of which the most important is food supply adequate in amount and in composition.

The present overcapacity game herds, inhabiting many parts of the Rocky Mountain parks, developed largely since 1930, at a time when predator control varied from none at all to light, with traps used infrequently, and poison strictly prohibited at all times.

There is thus further evidence here that, under certain circumstances, predators are powerless to prevent game irruptions. Under existing circumstances the predators present, coyote, wolf, fox, lynx, wolverine, mountain

lion, grizzly, and black bear, together are not taking the annual net increment to the game herds, nor even removing the cull group, a large part of which becomes carrion following death from disease, parasitism, or malnutrition.

Summary

This study deals with a wolf population with a density in Jasper Park of one wolf to between 87 and 111 sq. miles of potential range, which is reduced to about 10 sq. miles per wolf during late winter, by contraction of available range. The range is heavily populated with big game, including bighorn sheep, mountain goat, elk, moose, caribou, and mule deer, so heavily populated, in fact, that the cumulative use of the restricted winter ranges has engendered a serious depletion of the browse plants and grasses to the end that the reproductive success of much of the game is now very low. The winter range of the wolves supports a mixed game population of between 30 and 40 head per sq. mile, as counted in the spring, or roughly 300 to 400 surviving head of game per wolf.

The study area includes 7000 sq. miles of mountainous terrain in the Rocky Mountains, including extensive areas on both the east and west slopes.

Wolves are unevenly distributed over this immense area to a degree that leaves almost half the area without a wolf population, although game of all types is present in abundance in the wolf-free areas and the lesser carnivores such as coyote, mountain lion, and wolverine are fairly evenly distributed.

During the four years occupied by this study there was no appreciable change in the wolf population. Failure to breed, disharmonious proportion of the sexes and death from mange are believed to be mainly responsible, though man has removed some wolves.

The annual diet of wolves in Jasper and Banff National Parks has consisted of 80% big game, with elk alone contributing 47%. Mule deer contribute another 15%. It is particularly significant that although bighorn sheep were in great abundance they were very little hunted by the wolves. The wolves of the Rocky Mountain Parks thus demonstrate a marked proclivity toward the elk as a food animal and take elk in preference to sheep even when both are equally available and both are in excess of the carrying capacity of the ranges.

Eighteen per cent of the annual diet consisted of rodents, of which snowshoe hare and beaver were the two most important.

The wolf range in Jasper Park was excellent beaver range 15 years ago but the very high concentration of beaver that developed has removed the food trees from almost all readily available areas. Because of the action of elk and moose in killing all reproduction of such trees within two or three years of its establishment, new food trees are not appearing. Under such circumstances many of the remaining beavers are highly vulnerable to predation.

An examination of elk, and bighorn found dead from all causes, including wolves, reveals that the elk population is suffering a relatively heavy loss in

the prime age classes. The inference is made that wolves are not exerting a noticeable culling influence in their predation upon elk, so far as the term applies to the elimination of the weak. It is pointed out that in view of the overstocking of winter ranges as much as 50% of the current elk population can be considered as surplus and theoretically highly liable to predation. Losses to the sheep population, on the other hand, are confined largely to the young and old or diseased groups.

Vital statistics for game herds living with and without wolf pressure reveal that there is no discernible significant difference in the survival of young, or in the sex ratios within the two groups.

It is concluded that under existing circumstances the wolves are not detrimental to the park game herds, that their influence is definitely secondary, in the survival of game, to the welfare factors, of which the absence of sufficient suitable winter forage is the most important.

Any drastic reduction in the present elk herds, a reduction that is urgently needed, may quite well disturb the present balance and careful watch should be kept to the end that any major change in the position of the wolf relative to the other species of big game will be detected quickly.

Should the wolf turn to heavy predation upon mule deer, caribou, or moose, it may become necessary to attempt more intensive control.

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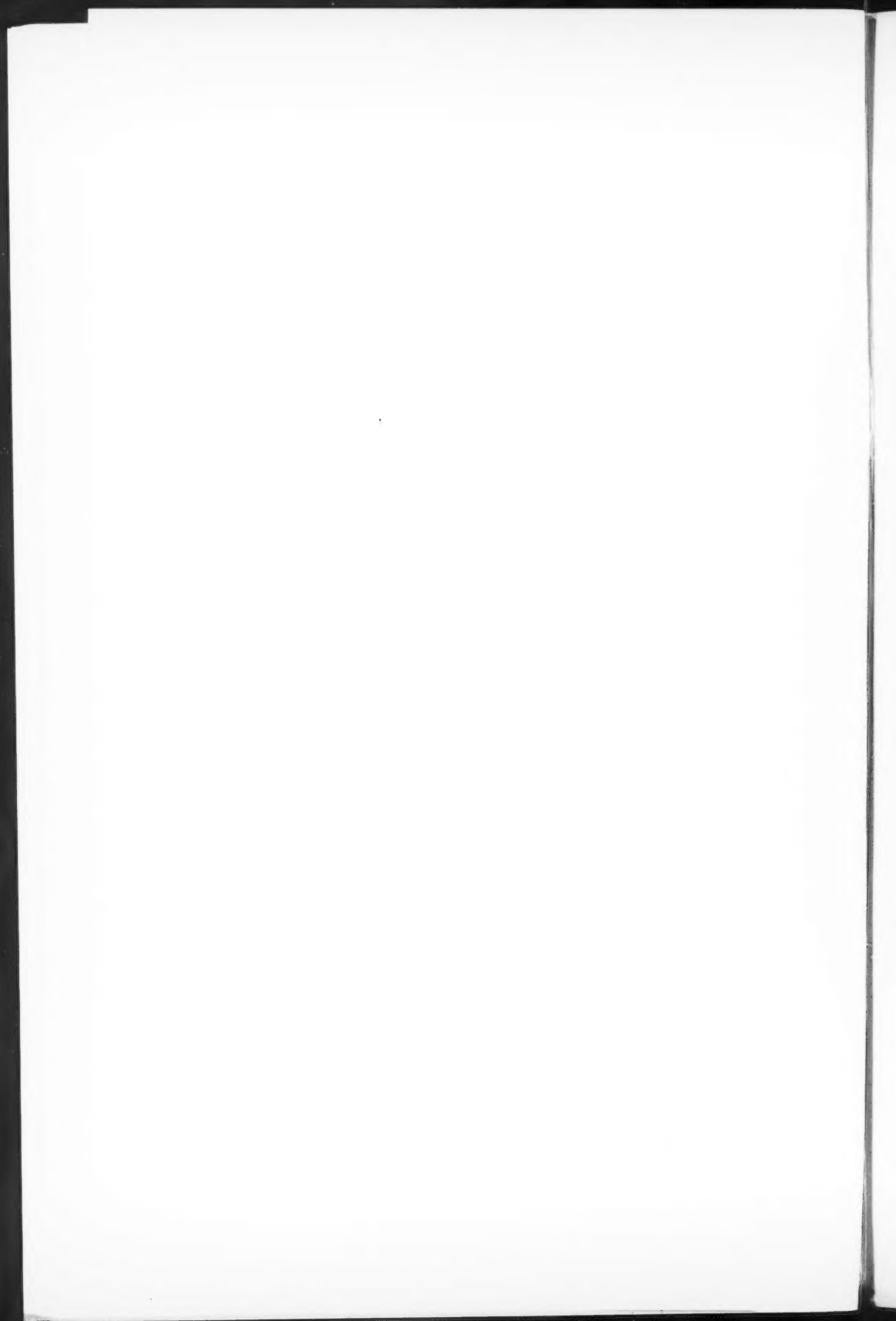
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